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Long-Term Changes in Fish Assemblage Structure Associated with Hydrological Alteration in the Lower Rio Grande/Rio Bravo del Norte (USA/Mexico)

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The lower Rio Grande watershed below Falcon Dam has been 95% developed for agriculture, urban, and industrial uses. The river has been extremely altered to make this possible, with the addition of two more downstream dams, a series of five rock weirs, and numerous water diversions. This regulation has resulted in an extremely altered flow regime and fish fauna since the early 1950s. There has been a significant general retreat and decline of primary freshwater fishes over time, and we identified three significantly different faunal groups across the fragmented watercourse. However, the overall species richness of the region did not change significantly over time, likely due to an ongoing upstream intrusion of estuarine and marine-derived taxa, as well as the increase in the number and spread of non-native taxa. Despite no overall change in species richness within the region, we identified a significant trend in the species richness of the two most diverse primary freshwater fish families, Leuciscidae and Centrarchidae. Leuciscid richness significantly declined and centrarchid richness significantly increased over the 68-year period. Fluvial native leuciscid species that require a natural flow regime became extirpated or extinct, while lentic-adapted native and introduced centrarchids have thrived. The flow regime of the lower Rio Grande has been severely altered since impoundment of Falcon Reservoir. Median monthly flows have declined for all months, maximum flows and high flow pulses have declined, and base flows have increased. Also noteworthy were the increased number of hydrograph reversals post-impoundment. The streamflow regime is of central importance in sustaining the ecological integrity of rivers, and its disruption in the lower Rio Grande corresponds to a vastly different contemporary fish fauna than what historically occurred.

THE composition of riverine fish assemblages and the persistence of fish species are closely linked with environmental conditions. River flow regimes can act as master variables controlling water quality, food resources, fish habitat, and can mediate biotic interactions (Poff et al., 1997). The alteration of flow regimes through damming and impoundment converts lotic ecosystems to lentic ecosystems, changes sediment transport, and reduces habitat and substrate diversity (Bunn and Arthington, 2002). These effects can result in significant changes to resident fish assemblages, including loss of biodiversity, species replacement, species extirpations/extinctions, and proliferation of introduced species (Vörösmarty et al., 2010; Tickner et al., 2020). Meta-analysis has shown that species richness and diversity decline in tropical and temperate rivers post-impoundment and there is a general increase in non-native and generalist species (Turgeon et al., 2019). Specialist species such as broadcast or substrate spawning fishes that require a natural flow regime or coarse substrates have been shown to decline in rivers post-impoundment (Perkin and Bonner, 2011; Taylor and Mayes, 2022). Lotic specialists (Taylor and Mayes, 2022) and diadromous fishes requiring river corridor connectivity (Gehrke et al., 2002) are vulnerable to extinction in impounded river systems due to loss of habitat and alteration of flow conditions.

The Rio Grande system drains a bi-national basin and forms an approximately 2000 km international border across Texas and northern Mexico. It is considered one of North America's most endangered river ecosystems due to extensive alteration of flow regimes and degradation in water quality, quantity, and habitat (Dettinger et al., 2015; Taylor et al., 2019). The lower Rio Grande delta region, from the Falcon Reservoir to the mouth of the river, is now 95% developed for agricultural, urban, and industrial uses, with few minimally impacted areas remaining intact (Contreras-Balderas et al., 2002). The lower Rio Grande is a low gradient river, dropping on average 0.18 m/km over its run and changing little in width or depth (Contreras-Balderas et al., 2002). The International Boundary Water Commission (IBWC) reported that discharge at the river delta in the 1990s was 32% that of the 1960s (Contreras-Balderas et al., 2002). The habitat in this region once commonly contained riffles, gravel, and sand banks in the 1950s, but this habitat is being lost due to siltation caused by flow regulation (Contreras-Balderas et al., 2002). In addition to habitat changes, water quality has changed drastically. Water quality at the confluence of the Rio San Juan has changed most notably in conductivity and dissolved ions of calcium, sodium, and chloride as a result of changes in rainfall, stream flow, and from saltwater encroachment from the delta (Contreras-Balderas et al., 2002). Flow dynamics, including the frequency

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and severity of flood events, and the long-term flow regime have been altered, affecting the movement of substratum material and reducing the complexity of river channel substrata including alteration of pool-riffle-run habitat structures (Contreras-Balderas et al., 2002; Lorang and Hauer, 2017). The cumulative result of these hydrologic impacts was on display in 2001 when the river failed to make it to the Gulf of Mexico.

Associated with the observed changes in river flows, habitat quality, and quantity has come a shift in the fish assemblages of the lower Rio Grande. Historically the fish fauna in this area has been relatively well studied with published surveys as early as 1892 (Evermann and Kendall, 1892). The lower portion of the Rio Grande was surveyed extensively by Robinson in 1959, with 20 sampling stations below the Falcon Reservoir. This lower segment of the river was surveyed again in 1975, then through the 1980s and into the 1990s (Edwards and Contreras-Balderas, 1991; Contreras-Balderas et al., 2002). In addition, Anderson et al. (1995) included lower Rio Grande sites in a state-wide study of changes in fish assemblages. These surveys have indicated major changes in ichthyofauna including a loss of native primary freshwater forms, the rise of invasive freshwater species, and encroachment of estuarine and marine forms (Edwards and Contreras-Balderas, 1991; Anderson et al., 1995). These biodiversity shifts are concurrent with changes in habitat quality and quantity, and the encroachment of saltwater from the estuary due to reduced flows. Species that were once common have declined, and there are some notable extirpations from the region including the leuciscids *Macrhybopsis aestivalis*, *Notropis jemezanus*, *Notropis orca* (extinct), and *Hybognathus amarus*.

Our objective was to conduct a contemporary survey of the fishes of the lower Rio Grande and to gather available ichthyological data from published papers and available databases from prior surveys of river habitats between Falcon Dam and the mouth to determine the magnitude of changes in the fish assemblages over the past 70 years. We also identify changes in river flows since the establishment of Falcon Reservoir and discuss how these changes have impacted lower Rio Grande species assemblages. We hypothesized that the richness of lotic specialist taxa like much of the native Leuciscidae will have declined over the timeseries, and lentic taxa will have increased in richness along with introduced taxa (e.g., Centrarchidae).

MATERIALS AND METHODS

Contemporary fish surveys (2017–2019).—To provide a contemporary, regional assessment of fish assemblages, we sampled 17 localities between Falcon Reservoir and Brownsville (Fig. 1; Supplemental Table 1; see Data Accessibility), accessed by truck or by boat (with the help/support of the Texas Parks and Wildlife Department and U.S. Customs and Border Protection). All sampling was conducted on the U.S. side of the river. Localities were sampled during extended base flows in summer months (May–August) of 2017, 2018, and 2019. Collections were made by seine (6.1 m × 1.8 m, 4.8 mm mesh), and all available habitat was sampled at each locality. Sampling was conducted for 30–60 min per locality depending on the amount of available habitat. We used a backpack electrofisher (Smith-Root LR24) for sampling in boulder-strewn substrates where pools are not easily seined, specifically below Anzalduas Dam and below Brownsville Irrigation District Weir #1 (Fig. 1). All fishes collected were anesthetized using sodium bicarbonate buffered MS-222 solution, fixed in 10% formalin, and preserved in 70% ethanol. Fishes were identified to species in the lab at the University of Texas Rio Grande Valley. For each locality where fishes were sampled, data on substrate types were recorded and photographs of each location were made. All activities were reviewed and approved under the Texas A&M University–Corpus Christi IACUC project ID# 03-17.

Historical fish datasets.—We compiled a historical dataset on fish distribution and abundance in the lower Rio Grande from reviews of published ichthyological surveys (Contreras-Balderas et al., 2002) and publicly available datasets, including the Fishes of Texas Project (Hendrickson and Cohen, 2015; https://www.fishesoftexas.org) and the US Environmental Protection Agency National Rivers and Streams Assessment (NRSA) dataset (EPA, 2009). The ichthyological collections in Contreras-Balderas et al. (2002) are extensive, including ten localities between Falcon Dam and Brownsville for a total of 59 individual samples. All collections in this reference are geo-referenced and were made on the Mexico side of the border from 1954 to 1996. The Fishes of Texas Project is maintained by Texas Natural History Collections at the University of Texas at Austin. This dataset contains records of museum-vouchered specimens and associated data from over 40 institutions based on specimens collected as far back as the mid-1800s. The EPA NRSA are nationwide surveys of ichthyofauna using standard field methods. Sampling in the lower section of the Rio Grande occurred in 2008 and 2009 (https://www.epa.gov/national-aquatic-resource-surveys/nrsa). These surveys were conducted using boat electrofishing, and fish species were enumerated at each sampling locality. Species identifications were conducted in the field by EPA "fish taxonomic specialists" and common names were assigned to each specimen; fish common names were designated based on Nelson et al. (2004). Voucher specimens were collected at 13% of NRSA localities. Of those, 12% (3,153) were reviewed by ichthyologists (EPA, 2016). Field identifications were determined to be 97% accurate to the genus level (EPA, 2016).

Analysis of fish assemblages.—Historic fish collection data were merged with contemporary fish collections. Historical datasets from the Fishes of Texas Project and the EPA were filtered to only include samples collected between Falcon Reservoir Dam (26°33′32″N, 99°09′53″W) and the mouth of the river. We additionally removed all samples which were collected outside of the mainstem of the river by mapping the sampling locations and manually removing those records from the dataset. Finally, only data collected after 1950 were retained since the availability of records in decades prior was very sparse. Additional filtering was performed on data gathered from the Fishes of Texas Project to remove sampling events which took place over multiple years or where only one species was collected or reported, based on the assumption that these could have been targeted collections, rather than community sampling, possibly biasing analyses of diversity. Finally, we aggregated sampling events into three broad river reaches based on those defined in Edwards and Contreras-Balderas (1991). They arbitrarily divided the lower section of the river into

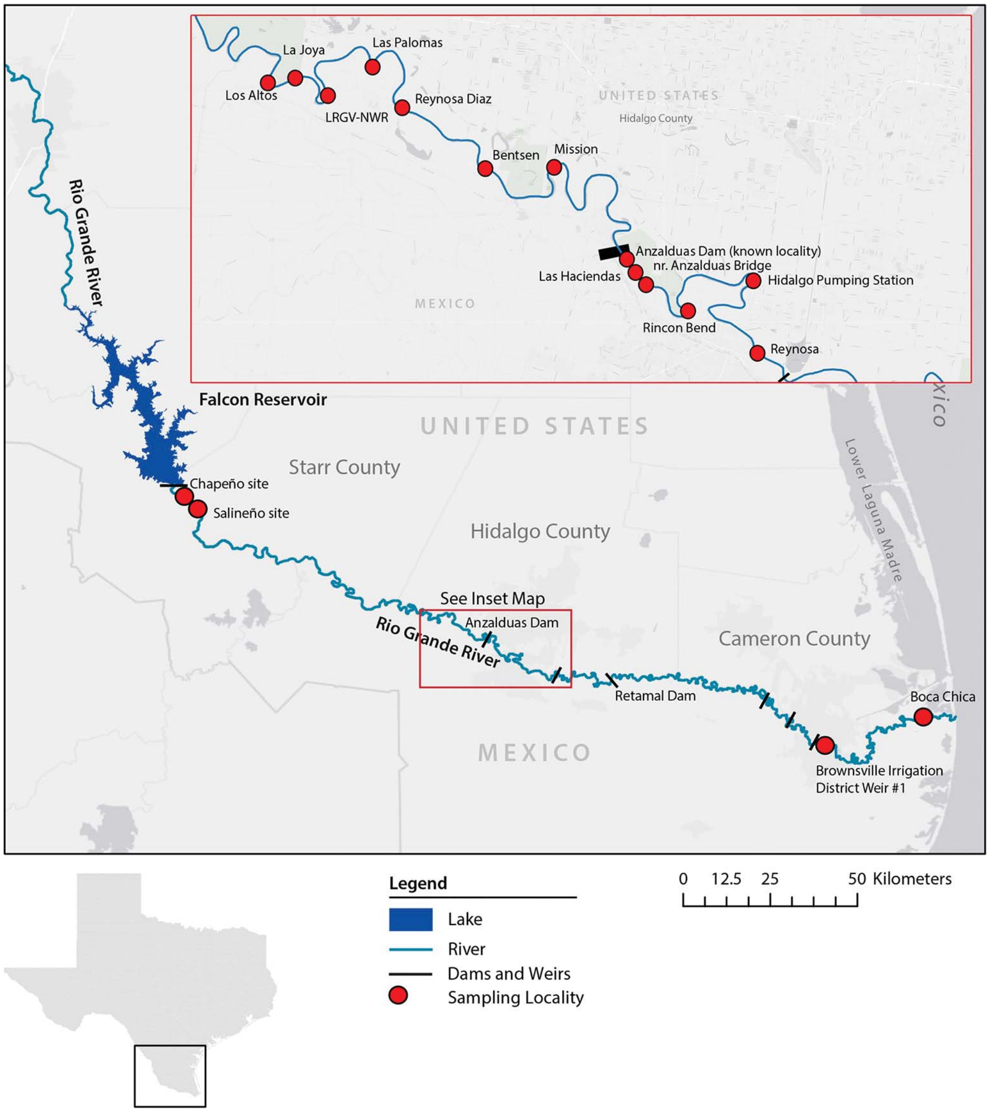

Fig. 1. Map of sampling locations (red dots) from sampling conducted in 2017–2019.

four roughly equidistant reaches (A through D) consisting of: (A) Falcon Reservoir; (B) Falcon Dam downstream to Anzalduas Dam; (C) Anzalduas Dam downstream to approximately the Brownsville Irrigation District weir #1, Brownsville, Texas; (D) Irrigation weir #1 to the mouth at Boca Chica (Edwards and Contreras-Balderas, 1991). For the purposes of comparison to their work, we retained the names of the reaches they devised. Our study encompasses only three of the four reaches they defined (B, C, and D).

Data analyses were performed on species occurrence data rather than abundance data for two reasons. First, early collections from the 1950s prior to the completion of the Falcon Dam are reported in Contreras-Balderas et al. (2002) as presence-only and so conversion of all other records to presence-only allows for direct comparison to this important pre-dam time point. Second, we have no meaningful way to control for effort in sampling across collections. Collections across the datasets were made using seine nets of various dimensions, backpack electrofishing, and boat electrofishing. Few of the records contain information on the amount of habitat surveyed or the length of time spent collecting. Since taxon abundance is highly sensitive to sampling effort, conversion to occurrence data reduces the effects of differences in effort on multivariate community analyses.

To visualize the sampling effort within each reach and species presence through time, we plotted all sampled species in taxonomic order separated by reach. To visualize changes in the community composition of collections through time, we ordinated each reach individually using a non-metric multidimensional scaling analysis (NMDS). We performed the NMDS at the family level, and due to the presence-only nature of much of the data, we used counts of the number of species in each family for a given sampling event. To identify if the community composition changed significantly across decades between reaches, we performed a permutational MANOVA (with 1,000 permutations) with years nested within decades and crossed with reach. Both the NMDS ordination and permutational MANOVA were performed using untransformed Bray-Curtis distance in VEGAN (Oksanen et al., 2010).

We chose to model the change in the two most species-rich families of primary freshwater fishes in the Rio Grande, the Centrarchidae and Leuciscidae. We modeled the annual mean species richness of sampling events which collected at least one of each family from the 1950s to the present and used a Bayesian generalized linear model with a negative binomial response distribution. We modeled a distinct change in mean annual richness for each family using uninformative priors. This model was created using the R package BRMS (Bürkner, 2018) and fit using the Hamiltonian Monte Carlo sampler in STAN (Carpenter et al., 2017). The model was run for 2,000 iterations which includes 1,000 warmup iterations on four independent chains. Mixing of chains and proper exploration of parameter space was confirmed by visually inspecting trace plots and ensuring the Rhat value equaled one (Vehtari et al., 2021). After fitting the model, we confirmed the assumptions that there were no divergent transitions, that none of the individual observations were overly influential using leave-one-out cross validation (Vehtari et al., 2017), and that the leave-one-out probability integral transform (LOO-PIT) fits a uniform distribution (Gabry et al., 2019). After confirming that the model adequately fit our data, we tested the *a priori* hypotheses that the richness of the family Leuciscidae is declining in the river over decades and that there has been a concomitant increase in richness of the family Centrarchidae determining the posterior probability of a negative and positive slope with respect to year. All analyses were performed in R version 3.5.2 using the TIDYVERSE packages as well as those previously mentioned (R Core Team, 2018; Wickham et al., 2019).

Assessing changes in river flows.—To determine the degree of hydrological alteration that has occurred in the lower Rio Grande after fragmentation of the river by Falcon Dam, we calculated flow duration curves from data collected pre- and post-fragmentation. Data used in all flow regime analyses were daily mean stream flows (cubic meters per second, cms). Daily flows were obtained for all years for which data are available from the International Boundary Waters Commission (IBWC) website for the flow gauge near Brownsville, Texas. Flow duration curves (FDCs) were constructed pre- and post-impoundment and visually assessed for differences. Flow duration curves demonstrate the percentage of time that flow in a river is likely to equal or exceed some specified value of interest.

Flow duration curves tell us little about how flow behavior varies seasonally or across years, so we performed a range of variability analysis (RVA). The RVA provides a means of assessing how flow behavior has changed based on a suite of 33 metrics from the following five categories: 1) magnitude of monthly water conditions, 2) magnitude and duration of annual extreme conditions, 3) timing of extreme water conditions, 4) frequency and duration of high flow pulses, and 5) rate/frequency of water condition changes. To identify changes in flow behavior after fragmentation, a non-parametric range of variability analysis (RVA) was used. To facilitate analyses, category boundaries were placed at 17 percentiles from the median yielding three categories of equal size: the lowest category contains all values less than or equal to the 33rd percentile; the middle category contains all values falling in the range of the 34th to 67th percentiles; and the highest category contains all values greater than or equal to the 67th percentile. The degree of non-attainment was determined and indicates the percentage of post-fragmentation years not meeting the RVA target (middle category). All flow analyses were conducted with Indicators of Hydrological Alteration (IHA) software, version 7.1 (The Nature Conservancy, 2009; https://www.ibwc.gov/home.html).

RESULTS

Changes in the fish assemblages in the lower Rio Grande (1951–2019).—In all, 212 species were collected or observed from 58 families and 20 orders of Chondrichthyes and Osteichthyes from 192 records spanning the years 1951–2019 (Fig. 2A, B; Supplemental Table 2; see Data Accessibility). The most species-rich families of primary freshwater fishes were the Leuciscidae (minnows and relatives; $n = 8$ species) and Centrarchidae (sunfishes, black basses, and relatives; $n = 8$ species; note: species counts includes both native and exotic species).

We found that the three reaches differed significantly in their assemblage composition (Fig. 2). NMDS analysis confirmed the presence of these three assemblages, and PERMANOVA results demonstrated that there were significant differences among reaches in assemblage structure (Table 1). Reach B (Falcon to Anzalduas) was distinct in that it harbored a greater proportion of primary freshwater fishes and noticeably lacked many euryhaline wanderers and marine-derived families (e.g., Elopidae, Engraulidae, Carangidae, Sciaenidae; Fig. 2). There were eight species of fishes that appear to be the most common and abundant taxa in Reach B, as they were found in at least 11 of 18 years of sampling and in all decades for which there are data; those species are: *Menidia beryllina*, *Astyanax mexicanus*, *Dorosoma petenense*, *Herichthys cyanoguttatus*, *Cyprinella lutrensis*, *Lepomis macrochirus*, *Micropterus salmoides*, and *Gambusia affinis*.

Reach D (Brownsville weir to the river mouth) was distinct from the other two reaches because it lacked most of the primary freshwater fishes (e.g., Leuciscidae, Ictaluridae, Centrarchidae) and was heavily dominated by marine-derived and euryhaline specialist families and species (Fig. 2). There are five species of fishes that appear to be the most common and abundant taxa in Reach D, as they were found in at least 17 of 29 years of sampling and in most decades for which there are data; those species are: *Mugil cephalus*, *Mugil curema*, *Citharichthys spilopterus*, *Anchoa mitchilli*, and *Lagodon rhomboides*.

Reach C (Anzalduas to Brownsville weir) was distinct as an intermediate between the other two reaches, harboring most of the primary freshwater families and species, as well as many secondary freshwater species (e.g., Atherinopsidae, Cyprinodontidae), diadromous species (e.g., Eleotridae), euryhaline wanderers (e.g., Clupeidae, Belonidae), and some marine-derived taxa (Fig. 2). There are 12 species of fishes that appear to be the most common and abundant taxa in Reach C, as they were found in at least 13 of 29 years of sampling and in all decades for which there are data; those species are: *Menidia beryllina*, *Dorosoma petenense*, *Dorosoma cepedianum*, *Astyanax mexicanus*, *Cyprinella lutrensis*, *Cyprinodon variegatus*, *Gambusia affinis*, *Poecilia latipinna*, *Poecilia formosa*, *Lepomis macrochirus*, *Herichthys cyanoguttatus*, and *Gobiomorus dormitor*.

Assemblage composition changed significantly over the 68-year time period that these records encompass. NMDS analysis of the three reaches indicated that assemblage composition shifted over time in all reaches (Fig. 3).

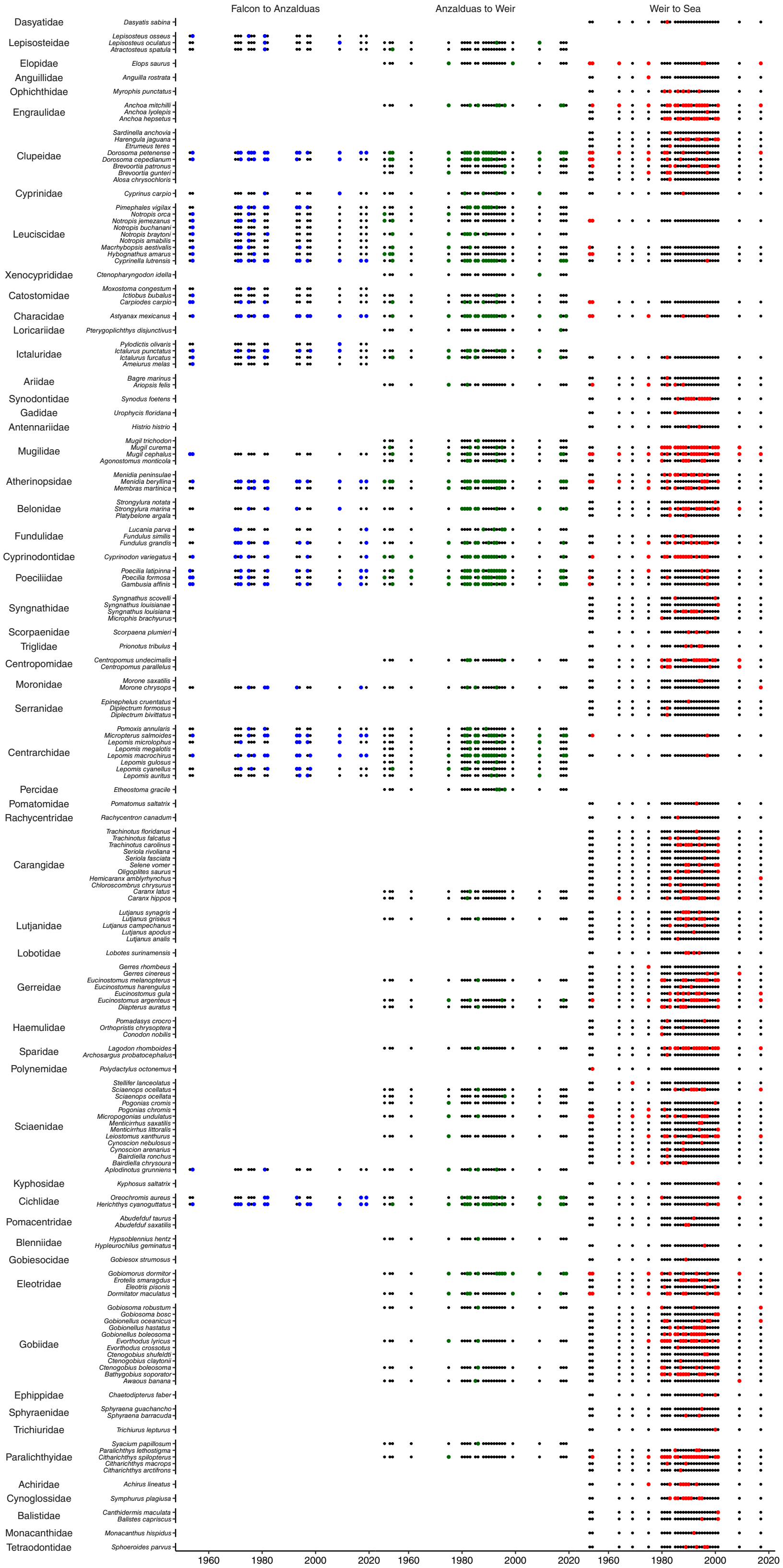

Fig. 2. Species observed in the lower Rio Grande by river reach and year. A line through time indicates a species has been found in that reach; black points indicate that there was a sampling event which occurred that year but the species was not observed; reach-specific colored points (blue = B; green = C; red = D) indicate that the species was collected that year in that reach. For a more detailed view, this figure is available as supplemental material (see Data Accessibility).

Table 1. Differences in fish community composition in space and time in the lower Rio Grande indicated by PERMANOVA analysis. Alpha value of 0.05 was determined as the cutoff for statistical significance.

	Df	SS	MS	*F*	r^2	*P*
Decade	6	5.481	0.9135	5.5623	0.11726	0.001
Reach	2	9.245	4.6223	28.1446	0.19778	0.001
Year(Decade)	30	8.661	0.2887	1.7578	0.18528	0.001
Reach * Decade	10	2.576	0.2576	1.5686	0.05512	0.005
Reach * Year(Decade)	22	4.192	0.1906	1.1603	0.08969	0.118
Residuals	101	16.588	0.1642	0.35487		
Total	171	46.743	1			

PERMANOVA analysis confirmed that these changes were significant (Table 1). The greatest changes in composition, as indicated by changes in positions of decadal centroids on NMDS 1 and NMDS 2, appear to have happened in the 1950s, 1960s, and 1970s in all reaches (Fig. 3). Changes in NMDS space in the last three decades of the series (1990s, 2000s, 2010s) appear to be generally smaller than changes in the early decades of the series (Fig. 3). These changes were marked by a significant increase over the 68-year period in the richness of centrarchid species collected per sampling event ($y = e^{-0.53+0.01*t}$; slope = 0.0112 [95% CI: –0.00316 to 0.0258]; posterior probability of positive slope = 0.9333; Bayes factor = 13.98). This was concomitant with a significant decrease in the richness of leuciscid species collected per sampling event ($y = e^{0.77-0.03*t}$; slope: –0.0291 [95% CI: –0.04274 to –0.0168]; posterior probability of negative slope = 1.0000; Bayes factor = ∞; Fig. 4). There are three species that appear to have once been widespread among all three reaches and abundant enough to be collected in numerous samples that exemplify the significant decline of leuciscids in the lower Rio Grande. *Macrhybopsis aestivalis* was previously collected in all reaches but was last observed in 1994 in Reach B, 1983 in Reach C, and 1953 in Reach D. *Hybognathus amarus* and *Notropis jemezanus* were both also widespread and abundant and both have not been observed since 1977 in Reach B and 1954 in both Reach C and D. Another notable cyprinid species that is known to be extinct is *Notropis orca* which was observed in Reaches C and B up until 1975.

Changes in river flows pre- and post-damming (1933–2012).—Flow duration curves for the Brownsville IBWC gage indicated that there were fewer high flows (eco-deficits), higher low flows (eco-surpluses), and no zero flows post-impact (Fig. 5). The RVA analysis confirmed that flows have been significantly altered post-impoundment. Twenty-eight of 33 variables across all five categories were not sufficiently attained (outside of the 34th–67th percentiles), and 26 of those had non-attainment rates greater than 50% (Table 2). Three parameters had 100% non-attainment (1-, 3-, and 7-day maximum; Table 2). Several general trends were evident and include reduced median flows for all months, reduced maximum flows, and increased minimum flows. Low pulse counts increased, and high pulse counts declined, but high pulse durations were longer. Also noteworthy were the increased number of hydrograph reversals post-fragmentation (Table 2).

DISCUSSION

We observed three distinct fish assemblages in the lower Rio Grande, one in each of the three reaches that were defined by Edwards and Contreras-Balderas (1991). This contrasts

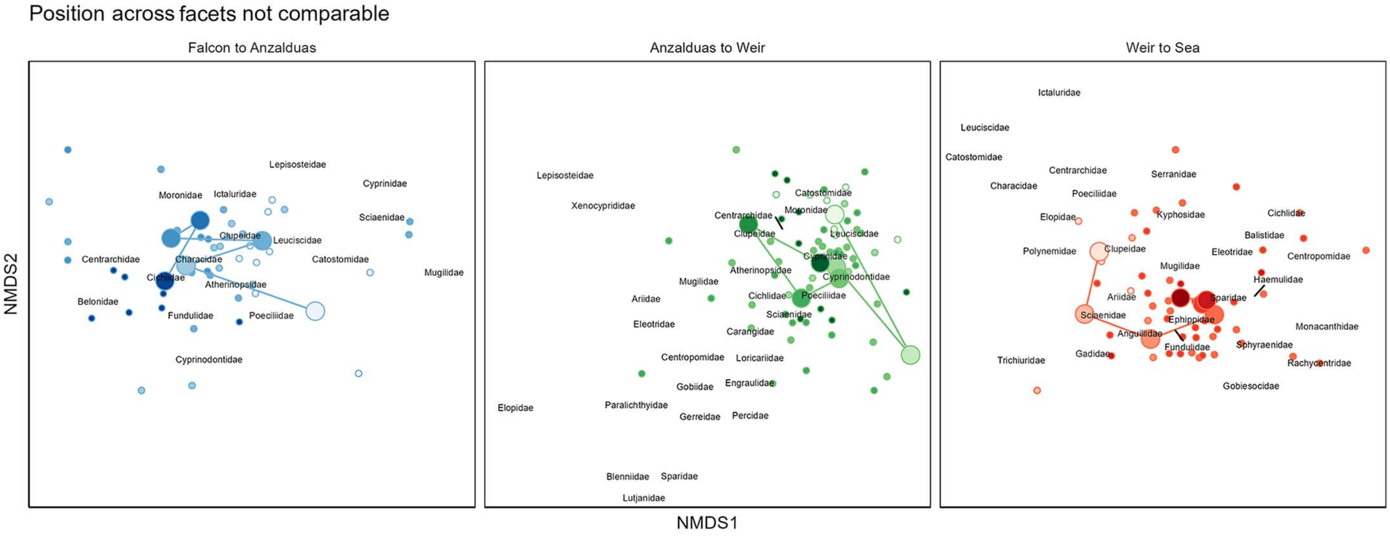

Fig. 3. Visualization of changes in fish community composition in NMDS space within the three reaches of the lower Rio Grande. Reach B (blue), Reach C (green), Reach D (red). Note that communities cannot be compared visually across facets. See PERMANOVA results for comparisons among communities. Small points mark the ordination of individual sampling events, while large points show the decadal centroid, with lighter shaded points indicating earlier decades and darkly shaded points being more recent decades.

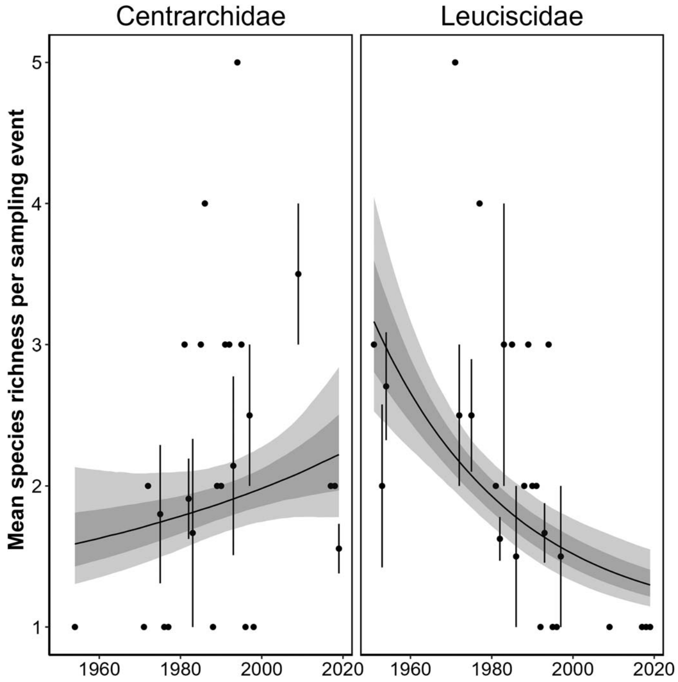

Fig. 4. Changes in mean species richness of the two dominant families of primary freshwater fishes in the lower Rio Grande, Centrarchidae and Leuciscidae, over 69 years of surveys. Points indicate the mean number of species observed each year with 68% and 95% credible intervals. The darkly shaded region shows the 68% credible region, and the lightly shaded region shows the 95% credible region around the estimated change in mean species richness.

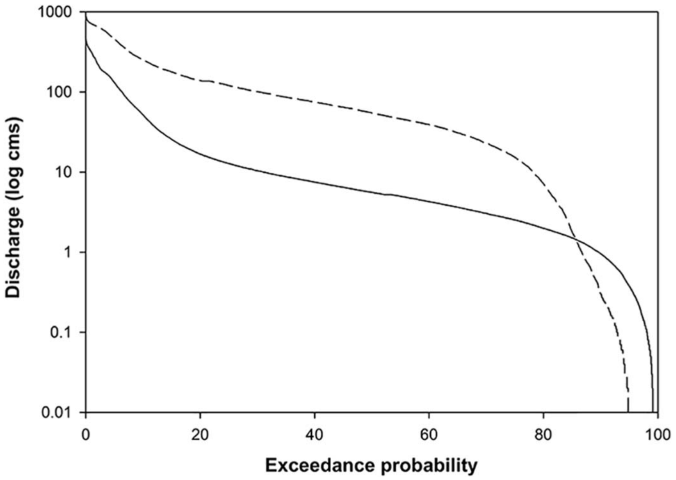

Fig. 5. Flow duration curves for the Rio Grande at Brownsville. Curves indicate the percent of time specified discharges were equaled or exceeded during a given period. Dashed line represents flow regime before impoundment by Falcon Reservoir (1934–1953), and solid line represents post-impoundment discharge (1955–2022).

with the findings of that study which concluded that there were two distinct faunas, an "upstream" and a "downstream" fauna. Part of the disparity between our result, and the conclusion of Edwards and Contreras-Balderas is due to the inclusion of downstream localities in the "arbitrary" definitions of the reaches. The primary differences in the fish fauna between Reach C (below Anzalduas Dam) and Reach B (above Anzalduas Dam) is the inclusion of many marine-derived taxa and euryhaline wanderers in the most downstream localities in Reach C (i.e., Carangidae, Lutjanidae, Gobiidae, Ariidae). The inclusion of these downstream sites in Reach C may create the appearance of three faunas when in fact there are two faunal types that mix in the downstream localities of Reach C. However, there were some species that appear to be quite common and/or widespread throughout Reach C that are not found in Reach B. For example, *Gobiomorus dormitor* was observed at three localities in Reach C in our contemporary surveys including sites only a few kilometers downstream from Anzalduas Dam. A precise break between the two faunas is fuzzy, but our findings broadly support the conclusions of Edwards and Contreras-Balderas (1991) and Contreras-Balderas et al. (2002) that there is a general retreat or decline of primary freshwater fishes and an increasing upstream intrusion of estuarine and marine forms in the lower Rio Grande.

Our analysis of fish data from all available sources showed a significant change in community composition from 1951–2019, with the largest changes occurring shortly after the completion of the Falcon Dam in 1953. The overall species richness of the river community did not change significantly over this time period. This is likely due to the ongoing upstream intrusion of estuarine and marine-derived taxa, as well as the increase in the number and spread of non-native taxa. However, this result hides more significant trends in the richness of the two most diverse primary freshwater fish families, Leuciscidae and Centrarchidae. Leuciscid richness significantly declined and centrarchid richness significantly increased over this 68-year period. It is notable that there were three abundant and widespread cyprinid species in the lower Rio Grande, *Macrhybopsis aestivalis*, *Hybognathus amarus* and *Notropis jemezanus*, all of which are pelagophilic in nature, that are almost certainly extirpated or at least have not been observed in several decades (Bestgen and Platania, 1991). Similar declines, most notably in the abundance and diversity of cyprinid species, were previously observed by Edwards and Contreras-Balderas (1991), Anderson et al. (1995), and Contreras-Balderas et al. (2002). This shift from dominance of one taxon to another indicates a major change in the freshwater fish fauna of the lower Rio Grande and may be symptomatic of the larger changes ongoing in the river ecosystem.

Since the Falcon Dam was completed in April 1954, river flows below the dam have been altered significantly. Large flood events have very rarely occurred since the dam was completed, and small flood events have significantly decreased in frequency and number. This coupled with a significant increase in baseflow and increases in water diversion for agricultural use has resulted in major changes to fish habitats. Siltation has increased (Contreras-Balderas et al., 2002) and there has been a loss of substrate and reach diversity. Riffles and gravel and sand banks that were once common in the 1950s (Contreras-Balderas et al., 2002) have been replaced by silt and mud, artificial concrete rip-rap, and/or the shells of invasive *Corbicula* spp. clams. We observed very little substrate diversity at contemporary sampling locations. Mud and silt were most common, but sites nearest the Falcon Dam (Salineño and Chapeño) had more diversity, with some riffles over bedrock, as well as *Corbicula* shell banks. Locations immediately below dams and weirs (Anzalduas and Brownsville Weir #1) also had man-made concrete rip-rap substrates.

Table 2. Results of the range of variability analysis (RVA) performed with indicators of hydrologic alteration (IHA) software (version 7.1) for the lower Rio Grande near Brownsville, Texas. The rate of non-attainment indicates the percentage of post-impoundment years not meeting the RVA target (34th–67th percentile).

	Pre-impoundment		Post-impoundment		Rate of non-attainment	
IHA groups	Median	CD	Median	CD	≤33%	≥67%
Magnitude of monthly water conditions						
October	127	1.596	5.95	2.85	76	
November	52.4	1.23	6.8	1.157	96	
December	47	1.217	5.76	1.359	96	
January	57.5	1.33	5.08	1.202	92	
February	53.4	1.344	5.835	1.019	92	
March	26.1	2.162	4.56	1.395	84	
April	23.65	1.603	4.01	1.377	86	
May	49.6	2.575	7.92	1.043	61	
June	52.1	1.706	6.85	1.273	80	
July	64.3	2.131	5.38	1.791	76	
August	63.4	1.867	4.13	1.202	61	
September	106.5	3.211	7.385	1.856	80	
Magnitude and duration of annual extreme conditions						
1-day minimum	0	0	0.31	2.968		
3-day minimum	0	0	0.5133	2.36		
7-day minimum	0.0386	232.1	0.9229	1.848		
30-day minimum	6.833	2.847	2.636	0.9422		
90-day minimum	21.93	1.574	3.957	1.017	96	
1-day maximum	694	0.2939	119	1.527	100	
3-day maximum	661	0.2491	103.7	1.798	100	
7-day maximum	566.4	0.4512	75.99	2.211	100	
30-day maximum	311.3	0.715	35.84	3.16	72	
90-day maximum	173.3	0.7107	19.42	3.175	72	
Number of zero days	4	4	0	0	57	
Base flow index	0.0003	226.2	0.04759	2.944		64
Timing of annual extreme water conditions						
Date of minimum	192	0.3661	163	0.3115		
Date of maximum	247	0.3361	260	0.3265		37
Frequency and duration of high flow pulses						
Low pulse count	6	0.6667	8	0.9375		55
Low pulse duration	6	1.208	15	2.108		40
High pulse count	8	0.625	0	0	94	
High pulse duration	5	0.5	8.5	3.206	90	
Rate/frequency of water condition changes						
Rise rate	5.4	0.6296	1.3	1.002	86	
Fall rate	−5.75	−0.548	−1.17	−1.004		92
Number of reversals	99	0.1212	124	0.1573		96

The changes in substrate and flow are likely large contributors to the faunal shift from a cyprinid- to a centrarchid-dominated primary freshwater fish assemblage. Changes in stream geomorphology as a result of changes in flood frequency and magnitude has resulted in shifts toward lentic-type habitats (Poff et al., 1997), contributing to the replacement of fluvial-specialist species with lentic-generalist species (Scott and Helfman, 2001). Additionally, four of the eight species of centrarchids observed were non-native (*Lepomis gulosus*, *Lepomis microlophus*, *Lepomis auritus*, and *Pomoxis annularis*), whereas none of the eight leuciscids observed were non-native. Introduced species that become established tend to have more generalist traits as well (Clavel et al., 2011).

It is an over-simplification to say that all leuciscids are fluvial specialists and all centrarchids are lentic generalists. For example, the Red Shiner, *Cyprinella lutrensis*, is a generalist species with broad tolerances (Perkin and Bonner, 2011) and one of the most commonly observed and widespread species in the river. Even post-dam construction, it is a definitive species for reaches B and C. Some centrarchids, such as the introduced *Pomoxis annularis*, have been only rarely observed (Fig. 2). However, we can generalize using species traits that have been classified for over 400 North American freshwater fishes (Goldstein and Meador, 2004). The centrarchid species observed in the lower Rio Grande are mostly nest-guarders with generalist nest substrate preferences, prefer finer substrate types (i.e., mud, silt, sand, gravel), lower flow conditions, and feed on a variety of food types (data source: https://water.usgs.gov/nawqa/ecology/pubs/index.html). The decline in flood events and the increase in siltation in the lower Rio Grande would likely benefit most centrarchid species. Comparatively, the leuciscids are defined mostly as pelagic or substrate spawners preferring coarser substrate type for their eggs (i.e., cobble, gravel, and sand). As a result, they tend to prefer moderate to fast currents and show an avoidance of natural and artificial lentic conditions that have become large in scale since dam construction. The changes in flow and substrate in the lower Rio Grande would likely have a stronger impact on the habitat availability and affect spawning of these leuciscids. Other possible causes for the decline have been hypothesized, including rising water temperatures, pollutants from agricultural runoff, and changes in salinity due to changes in river flows (Contreras-Balderas et al., 2002).

Similar changes in fish faunal assemblages have been observed in other river systems, and those changes were associated with changes in flow regime after damming. Several pelagophilic species have been extirpated from the lower Brazos River after extensive reservoir construction (Taylor and Mayes, 2022). In the Guadalupe River, mean flows increased and small and large flood events decreased in frequency after the damming of the Canyon Lake reservoir (Perkin and Bonner, 2011). Similar patterns were observed in the San Marcos River with the construction of flood control dams (Earl and Wood, 2002). This matches what we observed in the lower Rio Grande since the Falcon Dam was completed. In the Guadalupe and San Marcos Rivers, the fish fauna changed similarly to that of the lower Rio Grande, with the replacement of lotic-specialist species by lentic-generalist species (Perkin and Bonner, 2011), mainly due to declines in leuciscid species and increases in centrarchid species. They also observed that following periods of flooding (post-impoundment) generalist fish populations declined. This is further evidence that flow alteration in the lower Rio Grande is likely the primary contributor to the changes in fish fauna. This also suggests that if natural flow regimes could be restored or managed to mimic pre-impoundment flows, and if source populations existed or were repatriated for lost fluvial specialists, much of the original fish fauna could potentially rebound (Kinsolving and Bain, 1993). An overall whole-basin hydrologic model (including Mexico and U.S. waters) built to explore environmental flow restoration needs found that fallowing 18–26% of cropland and shifting to more profitable and less water-intensive crops could fill an environmental flow gap for late-summer low-flow conditions in the middle Rio Grande, while sustaining overall farm revenues (Richter et al., 2023). Given the climate-related water supply deficits of the Rio Grande system overall (Dettinger et al., 2015; Miyazono et al., 2015), and the continued growth and urbanization of the lower Rio Grande Valley, such ecological restoration will remain challenging for the Texas/Mexico transboundary waters.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2024024. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article.

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LITERATURE CITED

Anderson, A. A., C. Hubbs, K. O. Winemiller, and R. J. Edwards. 1995. Texas freshwater fish assemblages following three decades of environmental change. The Southwestern Naturalist 40:314–321.

Bestgen, K. R., and S. P. Platania. 1991. Status and conservation of the Rio Grande silvery minnow, *Hybognathus amarus*. The Southwestern Naturalist 36:225–232.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

Bürkner, P. C. 2018. Advanced Bayesian multilevel modeling with the R package brms. The R Journal 10:395–411.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1–32.

Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment 9:222–228.

Contreras-Balderas, S., R. J. Edwards, M. D. Loranzo-Vilano, and M. E. Garcia-Ramirez. 2002. Fish biodiversity changes in the lower Rio Grande/Rio Bravo, 1953–1996—a review. Reviews in Fish Biology and Fisheries 12:219–240.

Dettinger, M., B. Udall, and A. Georgakakos. 2015. Western water and climate change. Ecological Applications 25:2069–2093.

Earl, R. A., and C. R. Wood. 2002. Upstream changes and downstream effects of the San Marcos River of Central Texas. Texas Journal of Science 54:69–88.

Edwards, R. J., and S. Contreras-Balderas. 1991. Historical changes in the ichthyofauna of the lower Rio Grande (Rio Bravo del Norte), Texas and Mexico. The Southwestern Naturalist 36:201–212.

EPA (US Environmental Protection Agency). 2009. National Rivers and Streams Assessment Field Operations Manual. EPA-841-B-07-009. Office of Water, Office of Environmental Information, Washington, DC.

EPA (US Environmental Protection Agency). 2016. National Rivers and Streams Assessment 2008–2009

Technical Report. Office of Wetlands, Oceans and Watersheds, Office of Research and Development, Washington, DC.

Evermann, B. W., and W. C. Kendall. 1892. The fishes of Texas and the Rio Grande basin, considered chiefly with reference to their geographic distribution. Bulletin of the United States Fish Commission 12:57–126.

Gabry, J., D. Simpson, A. Vehtari, M. Betancourt, and A. Gelman. 2019. Visualization in Bayesian workflow. Journal of the Royal Statistical Society Series A: Statistics in Society 182:389–402.

Gehrke, P. C., D. M. Gilligan, and M. Barwick. 2002. Changes in fish communities of the Shoalhaven River 20 years after construction of Tallowa Dam, Australia. River Research and Applications 18:265–286.

Goldstein, R. M., and M. R. Meador. 2004. Comparisons of fish species traits from small streams to large rivers. Transactions of the American Fisheries Society 133:971–983.

Hendrickson, D. A., and A. E. Cohen. 2015. Fishes of Texas Project Database (version 2.0). Texas Advanced Computing Center, University of Texas at Austin. https://doi.org/10.17603/C3WC70

Kinsolving, A. D., and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. Ecological Applications 3:531–544.

Lorang, M. S., and F. R. Hauer. 2017. Fluvial geomorphic processes, p. 89–107. *In*: Methods in Stream Ecology, Volume 1: Ecosystem Structure. Third edition. F. R. Hauer and G. A. Lamberti (eds.). Academic Press.

Miyazono, S., R. Patino, and C. M. Taylor. 2015. Desertification, salinization, and biotic homogenization in a dryland river ecosystem. Science of the Total Environment 511:444–453.

Nelson, J. S., E. J. Crossman, H. Espinosa-Perez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada and Mexico. Sixth edition. American Fisheries Society, Special Publication 29, Bethesda, Maryland.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2010. Vegan: community ecology package. R package version 1.17-4. https://cran.r-project.org/web/packages/vegan/index.html

Perkin, J. S., and T. H. Bonner. 2011. Long-term changes in flow regime and fish assemblage composition in the Guadalupe and San Marcos rivers of Texas. River Research and Applications 27:566–579.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Richter, B. D., E. Prunes, N. Liu, P. Caldwell, D. Wei, K. F. Davis, S. Sandoval-Solis, G. R. Herrera, R. S. Rodriguez, Y. Ao, G. Lamsal, M. Amaya, N. Shahbol, and L. Marston. 2023. Opportunities for restoring environmental flows in the Rio Grande–Rio Bravo basin spanning the US–Mexico border. Journal of Water Resources Planning and Management 150:04023079.

Robinson, D. 1959. The ichthyofauna of the lower Rio Grande, Texas and Mexico. Copeia 1959:253–256.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26:6–15.

Taylor, C. M., and K. B. Mayes. 2022. Impact of hydrologic alteration on Brazos River pelagophilic minnows. Transactions of the American Fisheries Society 151:474–486.

Taylor, C. M., S. Miyazono, C. A. Cheek, R. J. Edwards, and R. Patino. 2019. The spatial scale of homogenization and differentiation in Chihuahuan Desert fish assemblages. Freshwater Biology 64:222–232.

The Nature Conservancy. 2009. Indicators of Hydrologic Alteration Version 7.1 User's Manual.

Tickner, D., J. Opperman, R. Abell, M. Acreman, A. H Arthington, S. E. Bunn, S. Cooke, J. Dalton, W. Darwall, G. Edwards, I. J. Harrison, K. A. Hughes, T. Jones, D. Leclere . . . L. Young. 2020. Bending the curve of global freshwater biodiversity loss—an emergency recovery plan. BioScience 70:330–342.

Turgeon, K., C. Turpin, and I. Gregory-Eaves. 2019. Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. Ecology Letters 22:1501–1516.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

Vehtari, A., A. Gelman, D. Simpson, B. Carpenter, and P. C. Bürkner. 2021. Rank-normalization, folding, and localization: an improved $\hat{R}$ for assessing convergence of MCMC (with discussion). Bayesian Analysis 16:667–718.

Vörösmarty, C., P. McIntyre, M. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. Reidy Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. Nature 467:555–561.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, and M. Kuhn. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.